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OCEAN (DE)OXYGENATION ACROSS THE LAST DEGLACIATION

INSIGHTS FOR THE FUTURE

BY SAMUEL L. JACCARD, ERIC D. GALBRAITH, THOMAS L. FRÖLICHER, AND NICOLAS GRUBER

ABSTRACT. Anthropogenic warming is expected to drive oxygen out of the ocean as the water temperature rises and the rate of exchange between subsurface waters and the atmosphere slows due to enhanced upper ocean density stratification. Observations from recent decades are tantalizingly consistent with this prediction, though these changes remain subtle in the face of natural variability. Earth system model projections unanimously predict a long-term decrease in the global ocean oxygen inventory, but show regional discrepancies, particularly in the most oxygen-depleted waters, owing to the complex interplay between oxygen supply pathways and oxygen consumption. The geological record provides an orthogonal perspective, showing how the oceanic oxygen content varied in response to prior episodes of climate change. These past changes were much slower than the current, anthropogenic change, but can help to appraise sensitivities, and point toward potentially dominant mechanisms of change. Consistent with the model projections, marine sediments recorded an overall expansion of low-oxygen waters in the upper ocean as it warmed at the end of the last ice age. This expansion was not linearly related with temperature, though, but reached a deoxygenation extreme midway through the warming. Meanwhile, the deep ocean became better oxygenated, opposite the general expectation. These observations require that significant changes in apparent oxygen utilization occurred, suggesting that they will also be important in the future.

INTRODUCTION AND CONCEPTS

Oxygen is a sparingly soluble gas, and its scarcity in the ocean affects the welfare and behavior of marine animals in

a large fraction of the ocean (Stramma et al., 2010). Although marine phytoplankton are responsible for about half of the planet's oxygen production, most of this photosynthetically produced

dissolved oxygen quickly outgasses, and the concentration remains within a few percent of saturation over most of the ocean surface (Garcia et al., 2010). Meanwhile, waters in the cold and dynamic environments of dense water formation tend to fall below oxygen saturation, given that it takes several weeks for gas exchange to compensate for the enhanced solubility stemming from cooling, combined with the often brief exposure of aged, undersaturated waters at the surface, particularly in the Southern Ocean (Gruber et al., 2001). As a result, while most of the waters near the ocean surface have a “pre-formed” oxygen concentration (i.e., the concentration these waters had when last exposed at the ocean surface) close to that of oxygen saturation, it can deviate by more than 20% from this value in some waters, especially those that are ventilated at very high southern latitudes (Ito et al., 2004).

In the ocean's interior, respiration by the marine ecosystem consumes the oxygen transported downward from the surface, with the most rapid rates of net oxygen consumption occurring just below the euphotic layer. Oxygen consumption goes essentially to completion in oxygen minimum zones (OMZs) that occupy about 1% of the modern ocean volume (Bianchi et al., 2012), after which denitrification must step in to provide oxidizing potential, with a host of biogeochemical consequences (see below). The OMZs are typically located in regions without unusually high rates of O_2 utilization but where water is poorly connected to the deep wintertime convection regions (Figures 1 and 2) at which oxygenated surface waters are injected into the ocean's interior (Luyten et al., 1983; Karstensen et al., 2008). In the Atlantic and Pacific, the most poorly connected waters are found in the relatively stagnant cyclonic gyres that exist north and south of the equator in the east at subsurface layers. These eastern tropical gyres, sometimes referred to as shadow zones, are distinct from the subtropical gyres, where waters are much better connected, owing to efficient transport and mixing from outcrop regions.

The dissolved O_2 concentration in the ocean's interior can therefore be conceptualized as the sum of three components: O_2^{sat} (saturation concentration), O_2^{diseq} (preformed disequilibrium, i.e., the difference of the oxygen concentration from the saturation concentration upon the water parcel's last contact with the atmosphere), and O_2^{bio} (net oxygen production minus consumption by the marine ecosystem below the surface layer, generally negative). While we can compute the O_2^{sat} value from temperature and salinity (with cold and fresh waters holding more oxygen), the value of O_2^{diseq} is

generally not known as its determination requires dedicated measurements, which are available from a handful locations only. As a consequence, neither the true preformed oxygen concentration nor the true biological utilization terms can be determined accurately from ocean interior measurements. Instead, the preformed oxygen concentration is nearly always approximated by the saturation concentration, even though it also includes the disequilibrium term O_2^{diseq} . Recognizing this shortcoming, the difference $O_2^{\text{sat}} - O_2$ is called the "apparent" oxygen utilization (AOU). O_2^{bio} becomes increasingly negative in the interior where accumulated respiration rates are high relative to the rate at which ocean circulation provides ventilated waters from the surface. In high-latitude waters, O_2^{diseq} is generally negative, particularly where oxygen-poor waters are exposed only briefly at the surface, and/or cooled very quickly prior to sinking. All three of the oxygen components are subject to change in the future (Keeling et al., 2010), and they have varied naturally in the past (Jaccard and Galbraith, 2012, and references therein).

OCEAN DEOXYGENATION IN A WARMING WORLD

It is expected that as the ocean warms in the future, its oxygen content will decrease, particularly in the upper ocean, a phenomenon referred to as "ocean deoxygenation" (Keeling et al., 2010; Matear and Hirst, 2003). Recent observations seem to indicate relatively large changes in dissolved oxygen over the past decades in various ocean basins (Stramma et al., 2008). But these changes remain subtle in the face of natural variability, so that great caution needs to be used when interpreting trends over 20 years or less in the context of global

warming (Frölicher et al., 2009).

The future evolution of the ocean's oxygen content under anthropogenic climate change depends on three factors: (1) the degree of ocean warming, (2) changes in oxygen demand resulting from changes in growth and respiration rates, and (3) changes in ocean circulation and mixing. Projections with current-generation Earth system models as well as theoretical arguments suggest a consistent trend toward lower oxygen content of the global ocean (Sarmiento et al., 1998; Cocco et al., 2012; Bopp et al., 2013). For the high greenhouse gas emission scenarios (such as RCP 8.5 with a radiative forcing target of 8.5 W m^{-2} in year 2100), where surface ocean warming approaches 3°C , the total oceanic loss of oxygen by the year 2100 amounts to between 3% and 4%. But even for conservative emission scenarios (e.g., RCP 2.6), where surface warming remains below 1°C relative to present, the ocean is projected to lose about 2% of its current oxygen inventory by the end of this century (Bopp et al., 2013).

In nearly all models, this trend is predominantly driven by changes in ocean circulation and mixing, particularly the increase in upper ocean stratification, which allows the O_2^{bio} demand to accumulate in the ocean interior. This trend is to a substantial degree reinforced by upper ocean warming, which reduces O_2^{sat} . In fact, this reinforcement tends to lead to a rather consistent and uniform relationship between ocean heat uptake from the atmosphere and loss of oxygen from the ocean, with a ratio of about 4 to 6 $\text{nmol } O_2 \text{ J}^{-1}$, as evidenced from both models (Plattner et al., 2002) and observations (Keeling et al., 2010; Stendardo and Gruber, 2012). In contrast, the modeled contribution of changes in export production affecting

the rate of O_2^{bio} and changes in the O_2^{diseq} to the overall changes in oxygen are comparatively small.

Current models agree remarkably well on the global evolution of ocean deoxygenation, but they show large differences at the regional level (Bopp et al., 2013; Cocco et al., 2012). Regions of consistent deoxygenation for the next 100 years are the near-outcrop waters of the well-ventilated thermocline in the upper 600 m and in high-latitude regions (Figure 3). In contrast, the deep ocean generally shows little or no change in oxygen, and OMZs vary in an inconsistent manner (Figure 3). This inconsistency is particularly evident if deoxygenation is analyzed in terms of changes in volume for a particular range of oxygen. The most recent set of Earth system models project changes for the hypoxic

class water volume ($O_2 < 50 \mu\text{mol kg}^{-1}$) from -30% to $+15\%$, and for the anoxic class ($O_2 < 5 \mu\text{mol kg}^{-1}$) from -10% to more than $+40\%$.

The reasons for these large regional differences in the future evolution of oceanic oxygen content are associated with different mechanisms that control the oxygen concentrations and different circulation/mixing time scales (Sarmiento and Gruber, 2006). The oxygen content of the well-ventilated thermocline and of high-latitude regions is determined by the balance between high demands for oxygen from remineralization of organic matter and relatively rapid ventilation of these waters from the outcrop. In contrast, the deep ocean is governed by small oxygen utilization rates and very slow ventilation. As a result, the two regions react differently

to transient increases in stratification or, in other words, transient decreases in the resupply of oxygen by circulation and mixing. Given their high oxygen utilization rates, the oxygen concentrations in the thermocline and high-latitude regions respond very quickly and strongly to changes in resupply, while it takes centuries for the deep ocean to respond.

The governing balance that determines OMZ oxygen concentration is more complex. OMZ locations are largely determined by the existence of relatively isolated shadow zones, but their extent and oxygen concentration is governed by complex oxygen resupply processes that involve strong zonal jets and eddy-driven mixing (Karstensen et al., 2008). These processes are very difficult to capture with the current,

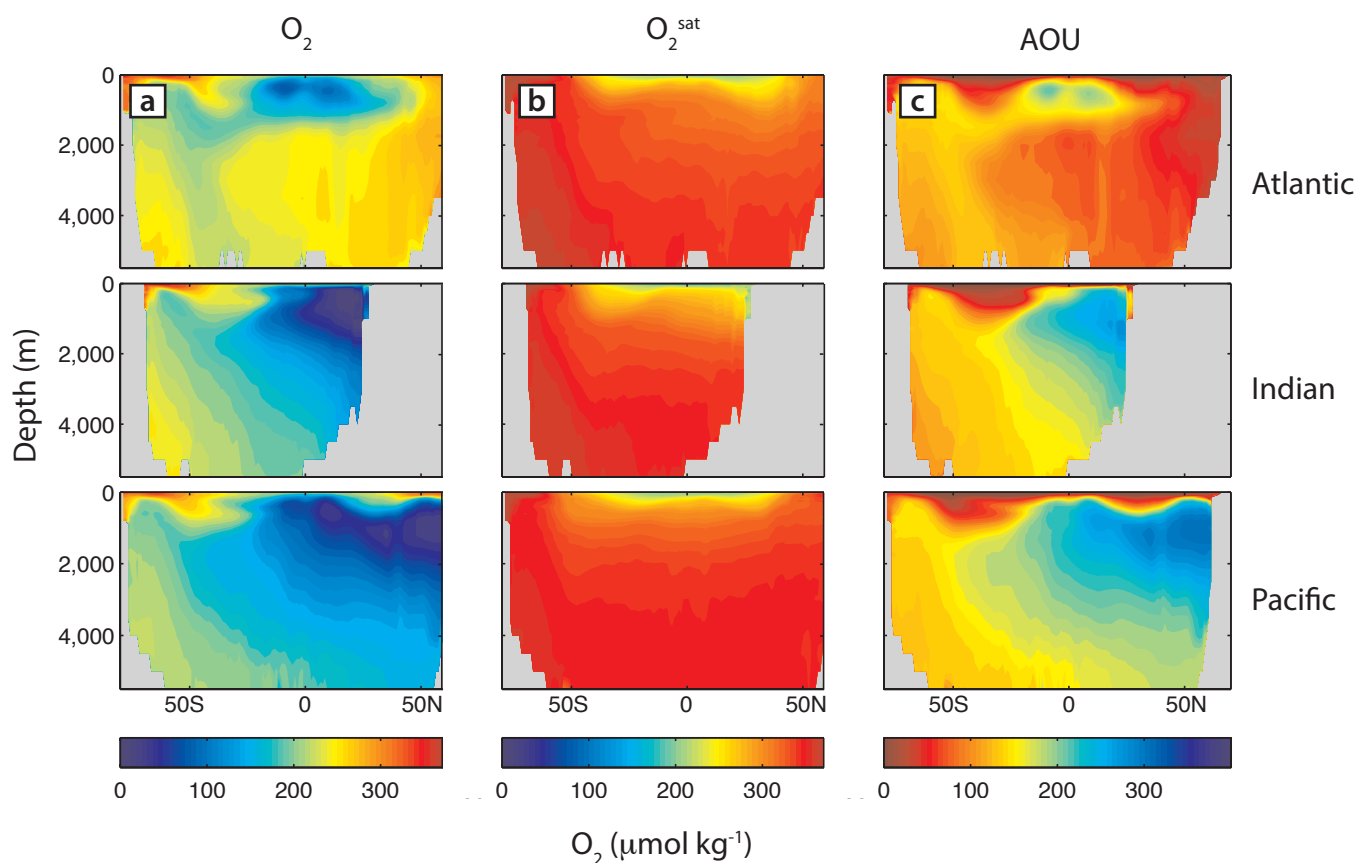


Figure 1. Present-day zonal-mean of (a) oxygen, (b) oxygen saturation (O_2^{sat}), and (c) apparent oxygen utilization (AOU) for all three ocean basins, based on the World Ocean Atlas 2009 (Garcia et al., 2010).

relatively coarse-resolution global Earth system models, resulting in different and largely inaccurate representations of modern oxygen minimum zones in these models (Cocco et al., 2012). These problems persist when the models are used to project future changes in these regions, limiting our ability to assess how OMZs will develop in the future. But perhaps the oxygen changes of the past ocean will help us to better constrain the future.

PERSPECTIVE FROM THE PAST

Seawater has not, in itself, been recovered in a biogeochemically unaltered state from any available reservoirs. Thus, there is no analog to the CO₂, CH₄, or N₂O content of air bubbles trapped in polar ice, which can be used to directly sample past variations in atmospheric greenhouse gas concentrations. Rather,

reconstructions of the past oxygenation of the ocean rely on sedimentary proxies of benthic oxygen depletion, all of which essentially record the redox state at the sediment-water interface. Variations in sedimentary redox state could be caused either by changes in the magnitude and distribution of biological export or by changes in bottom water oxygenation. Here, we make use of the three most common proxies: laminations, benthic foraminiferal species assemblages, and redox-sensitive trace metals (see Box 1).

Deglacial Changes in Oxygenation

The geological record provides a perspective on how oceanic oxygen content responded to prior episodes of climate change. These past changes tended to be much slower than the current, anthropogenic change, so they do not provide a direct comparison. Nonetheless, they can help to gauge sensitivities and point toward potentially dominant mechanisms of change. Here, we present an updated compilation of more than 100 proxy records of oxygenation

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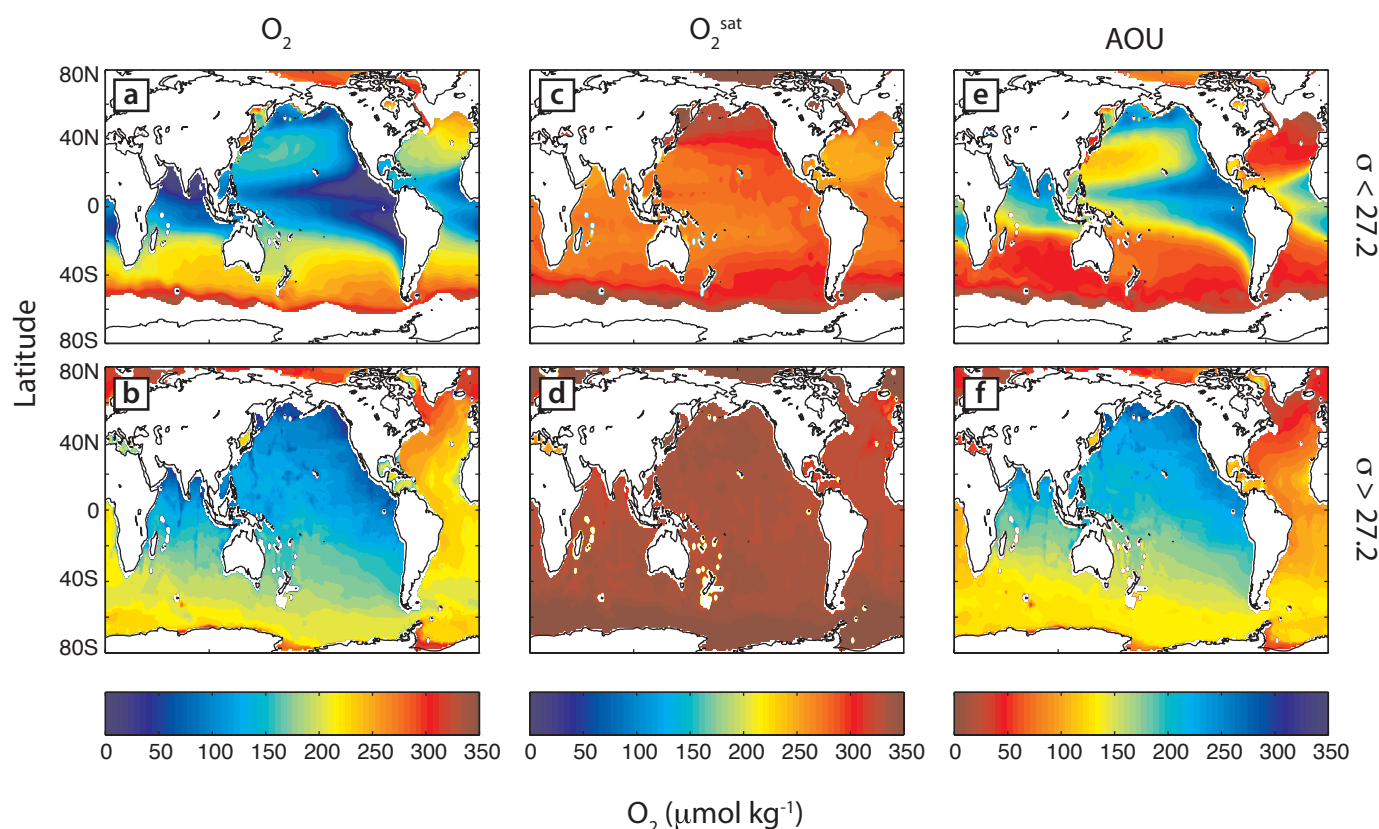


Figure 2. Present-day distribution of (a,b) oxygen, (c,d) oxygen saturation (O_2^{sat}), and (e,f) apparent oxygen utilization (AOU) based on the World Ocean Atlas 2009 (Garcia et al. 2010). Data are shown below 100 m and are averaged for $\sigma < 27.2$ and for $\sigma > 27.2$.

covering the last glacial termination—the transition from the last ice age to the Holocene, the current interglacial (for a detailed methodological description, see Jaccard and Galbraith, 2012).

We start by considering the change between the Last Glacial Maximum (LGM) and the Holocene to provide a perspective on how the oxygenation of a warm ocean might differ from that of a cold ocean, at steady state. The LGM, a time interval of a few millennia centered about 21,000 years ago, was characterized by the presence of large continental ice sheets in both hemispheres, and the global average temperature was colder by about 3–4°C (Shakun et al., 2012; Figure 4). The resulting significant expansion of sea ice, combined with drastic cooling in polar regions and changes in winds, would have altered the global subsurface ocean circulation (Adkins, 2013). The Holocene (i.e., the

last 10,000 years), on the other hand, has been a period of relative climate stability (Marcott et al., 2013), with the most dramatic deglacial changes running to completion and the remaining ice sheets slowly receding.

From the LGM to the Holocene, rising temperatures would have decreased O_2^{sat} (Galbraith et al., 2004). To roughly illustrate this effect, we calculate O_2^{sat} change for a ~ 1 unit reduction of salinity combined with a temperature rise of 1.5–2°C, as shown by global surface ocean temperature changes (MARGO Project Members, 2009). This is a conservative estimate, given that ocean temperature reconstructions at some deep sites suggest warming of more than 3°C (Adkins et al., 2002). The result, shown in Figure 5, is a global decrease of oxygen solubility of up to 20 $\mu\text{mol kg}^{-1}$ in the Holocene compared to the LGM, representing about 5% of the saturation

concentration. This relatively small magnitude of change might be expected to challenge the ability of oxygenation proxies to resolve it. However, the multiproxy data compilation, plotted on top of the expected O_2^{sat} change, shows a clear decrease of oxygenation in the upper Pacific Ocean, in keeping with the sense of change expected for O_2^{sat} for the deglaciation. Meanwhile, the rest of the ocean tends to show an increase of oxygenation—the opposite expected from the change of O_2^{sat} alone. Importantly, the deep ocean (below 2–2.5 km) appears to have had lower oxygen concentrations during the LGM (Sarkar et al., 1993; Mangini et al., 2001; Galbraith et al., 2007; Bradtmiller et al., 2010), consistent with greater respired carbon storage there that may have contributed to the low glacial atmospheric CO_2 (Jaccard et al., 2009; Sigman et al., 2010). Although it is not yet possible to quantify deep ocean O_2 concentration during the LGM, proxy sensitivities would suggest it was 50 to 150 $\mu\text{mol kg}^{-1}$ less than the modern concentration (Jaccard et al., 2009). These observations require that LGM-to-Holocene changes in O_2^{bio} and/or O_2^{diseq} were larger, and of opposite sign, to the change in O_2^{sat} over much of the deep ocean. In other words, the AOU during the Holocene appears to be smaller than it was during the LGM throughout the ocean, with the notable exception of the Pacific thermocline, where the world's largest hypoxic zone currently resides.

A few of the glacial-interglacial changes in global biogeochemistry that have been suggested could be consistent with these observations. It has been noted that deglacial warming would have decreased the efficiency of vertical carbon export from the surface to the ocean interior due to the presumed

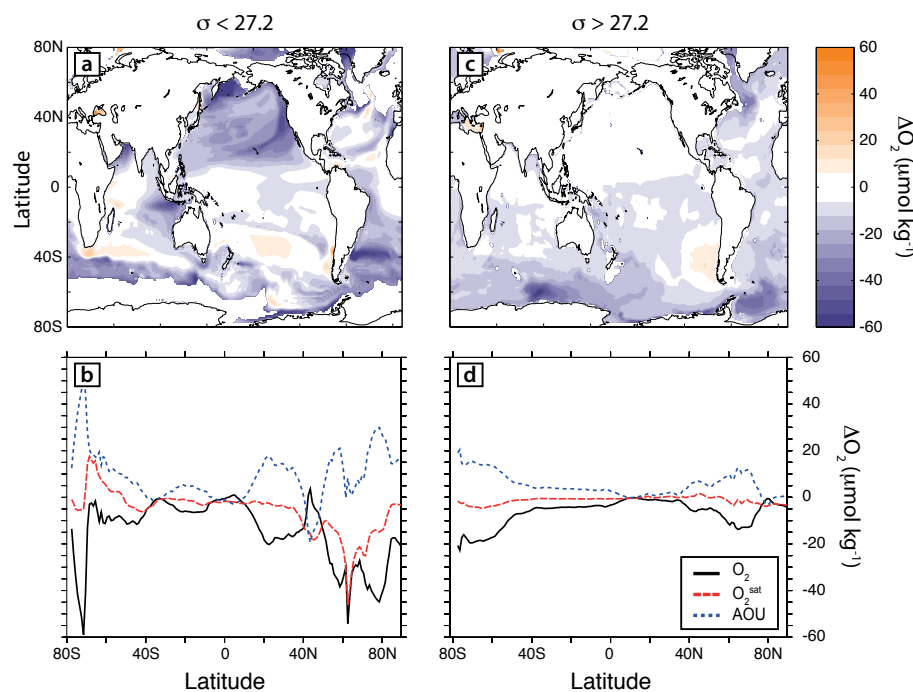


Figure 3. Changes in oxygen over the period 1990 (represented by mean of period 1981 to 2000) and 2090 (represented by mean of period 2081 to 2100) simulated by the Geophysical Fluid Dynamics Laboratory model ESM2M (Dunne et al., 2012; Gnanadesikan et al., 2012). Data are shown below 100 m and are averaged in (a,b) for $\sigma < 27.2$ and for $\sigma > 27.2$ (c,d).

temperature dependence of the remineralization rate of sinking organic matter (Matsumoto, 2007). This would have caused O_2^{bio} to become less negative in the deep ocean, while it would have become more negative in the upper ocean, alongside an increase in nutrients there. The nutrient concentrations of the upper ocean indeed appear to have increased from LGM to Holocene (Boyle, 1988). Consistent with this observation, paleoceanographic proxy records from OMZs have been interpreted as showing general intensification of oxygen depletion across the deglaciation (Jaccard and Galbraith, 2012, and references therein). This occurred even though biological production may have decreased at low latitudes as a result of slackening wind-driven upwelling (Kohfeld et al., 2005).

In addition, the last deglaciation provides a unique perspective on transient changes between the two steady states. Deglaciation did not follow a smooth, gradual progression;

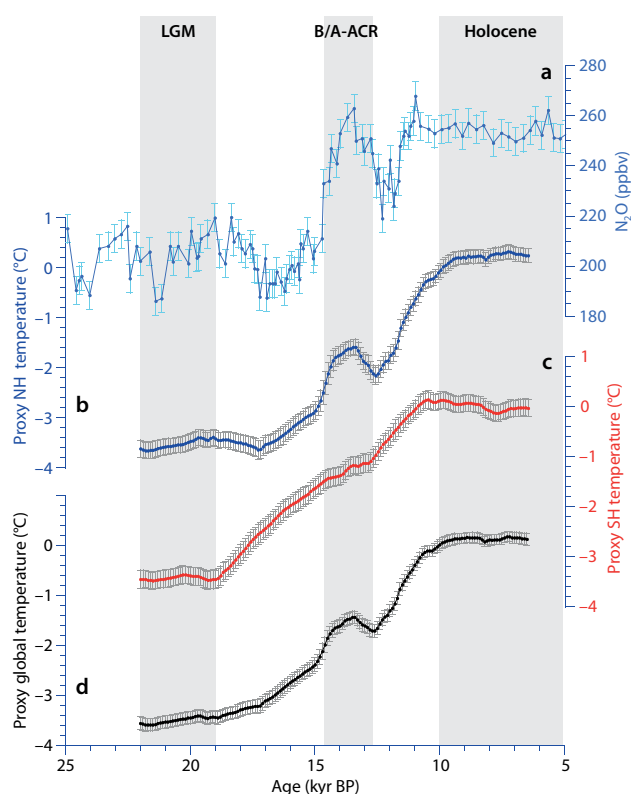


Figure 4. Records of changing climate and atmospheric greenhouse gas concentrations across the last glacial termination. The deglacial progression of (a) atmospheric N_2O concentration from the Dome C and Dronning Maud Land (EDML) ice cores (Schilt et al., 2010), (b) Northern Hemisphere proxy temperature stack, (c) Southern Hemisphere proxy temperature stack, and (d) global proxy temperature stack (Shakun et al., 2012). The gray shadings indicate the time intervals considered for the quantitative changes in oxygenation proxies. LGM = Last Glacial Maximum. B/A-ACR = Bølling/Allerød-Antarctic Cold Reversal.

BOX 1. TOOLBOX – BENTHIC OXYGENATION PROXIES

High sedimentation rate and extreme oxygen deficiency typically suppress sediment reworking by burrowing organisms. Absence of sediment mixing allows the seasonal cyclicity in marginal sediment supply to be preserved as thin, typically millimeter-scale laminations. The development of laminations depends on the nature of the sedimenting material and is only sensitive to oxygen at very low dissolved oxygen concentrations (i.e., close to anoxia). The absence of laminations could reflect a lack of regular variations in sedimenting material, but the presence of laminations is an unambiguous testimony of bottom water oxygenation levels $< 5 \mu\text{mol kg}^{-1}$ (van Geen et al., 2003).

Foraminifera dwelling at or just below the sediment-water interface are particularly suitable for monitoring abrupt climate change and oxygen levels because many species are known to be opportunistic, rapidly responding to environmental change, including bottom water oxygenation and organic matter availability at the seafloor (Corliss, 1985).

Many trace elements are present in seawater either in soluble form or adsorbed onto particles. Under oxygen-depleted conditions, sedimentary redox-sensitive trace metal enrichments (such as V, Mn, Mo, Cd, Re and U) may occur through diffusion across the sediment interface and precipitation as mineral phases at reducing horizons within the sediment (Tribouillard et al., 2006). It has been generalized that redox-sensitive metals precipitate as authigenic mineral phases in sediments where oxygen penetrates to less than 1 cm (Morford et al., 2005), and dissolved oxygen levels of overlying bottom waters exceeding $50 \mu\text{mol kg}^{-1}$ are rarely observed (McManus et al., 2005).

All three proxies have their shortcomings and are sensitive to changes of oxygen over differing concentration ranges. In addition, their behavior will vary at each site, depending on local sediment dynamics. However, these individual weaknesses are largely independent of each other and, thus, including all three proxy types, we can infer a relatively robust qualitative representation of past changes in benthic oxygenation. A more quantitative assessment of the changes, however, is not yet possible. Because the oxygenation proxies are most sensitive at low oxygen concentrations (typically $< 20\%$ of saturation), the compiled oxygenation changes are biased towards the Indo-Pacific where oxygen is, on average, lower. In addition, most records are located in continental margin settings, where higher sediment accumulation rates provide the temporal resolution required to resolve millennial-scale changes in bottom water oxygenation.

rather, a period of decelerated warming interrupted the trend near the deglacial midpoint (Shakun et al., 2012; Figure 4). This interval, known as the Bølling/Allerød-Antarctic Cold Reversal (B/A-ACR, 14,500 to ~12,500 years ago), was initiated by an abrupt, transient warming event in the Northern Hemisphere when the Atlantic Meridional Ocean Circulation (AMOC), greatly weakened throughout most of the deglaciation, was abruptly reinvigorated (McManus et al., 2004). The strengthened AMOC transported heat from the Southern Hemisphere to mid and high northern latitudes, causing

a corresponding cooling in the Southern Hemisphere. This interruption was one of many such AMOC oscillations that punctuated glacial ice core records with dramatic temperature swings between the two hemispheres, known as the bipolar seesaw (Stocker, 1998). After the B/A-ACR, the bipolar seesaw swung back and forth once more before settling into the stable Holocene about 4,000 years later.

Because high sedimentation rates and well-constrained sedimentary age models are required in order to resolve the B/A-ACR, fewer records are suitable to compare oxygenation during this period

with the Holocene. Nonetheless, the available records show a consistent pattern, with the largest volumetric expansion of oxygen-depleted water masses during the rapid Northern Hemisphere warming at the onset of the B/A-ACR. At this time, oxygen concentrations plummeted throughout the Indo-Pacific above 2,500 m, presumably linked to the simultaneous reinvigoration of the AMOC (Jaccard and Galbraith, 2012). Surprisingly, however, the North Pacific then showed a subsequent increase in oxygenation from the B/A-ACR to the Holocene (Figure 5b), despite the continued global average temperature rise of 1–2°C and similar AMOC strength between the two periods (Figure 4). Two mechanisms are proposed for the mid-deglacial oxygen nadir observed in the intermediate-depth Indo-Pacific.

First, enhanced local stratification due to the rapid freshening and warming of the sea surface could have caused a transient large decrease in the downward supply of oxygen to the thermocline. Although a colder global ocean may be generally more stratified than a warmer ocean at steady state (Winton, 1997), warming (and freshening) the ocean rapidly from above tends to stratify the upper ocean transiently, until the deep ocean can accommodate and dissipate the heat from above by downward mixing. The lag between surface- and deep-ocean warming can amount to many centuries. Moreover, sea surface warming at sites of subsurface water formation—in the Sea of Okhotsk (Ternois et al., 2000) and in the Gulf of Alaska (Davies et al., 2011)—combined with increased oxygen demand due to high export production would have conspired to severely reduce the oxygen concentration of North Pacific Intermediate Waters (NPIW) (Crusius et al., 2004; Jaccard and

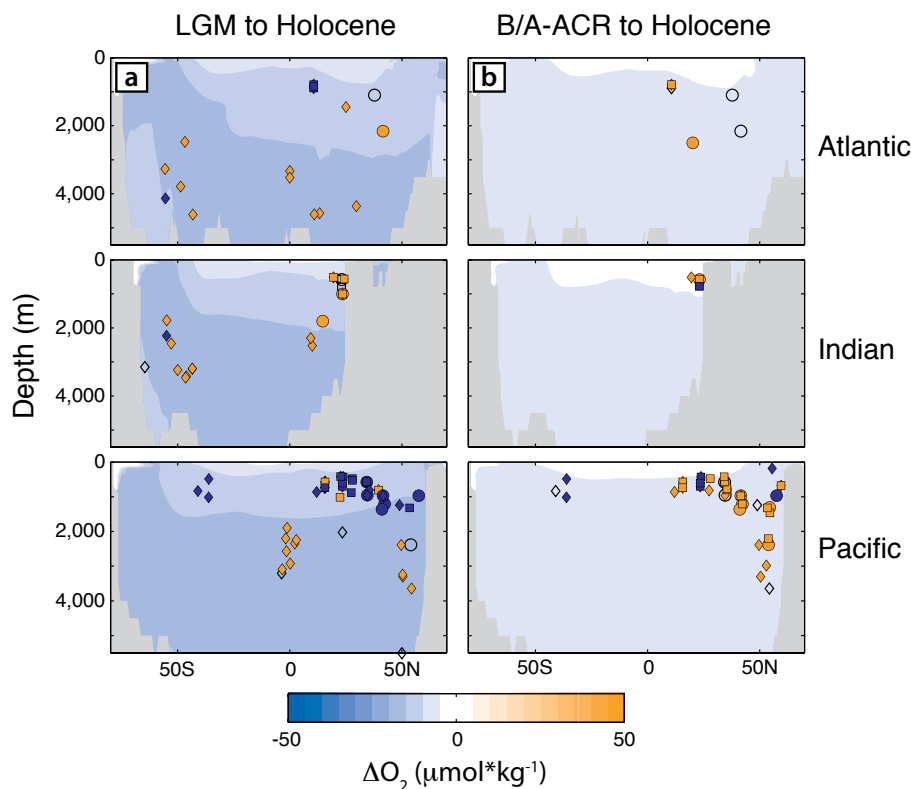


Figure 5. Qualitative changes in benthic oxygenation proxies between (a) the Last Glacial Maximum (LGM; 22,000–20,000 years ago) and the Early Holocene (10,000–5,000 years ago), and (b) the Bølling/Allerød-Antarctic Cold Reversal (14,700–12,500 years ago) and the Early Holocene (10,000–5,000 years ago). The multiproxy data compilation is plotted on top of the expected O_2^{sat} change. The symbols illustrate the proxies used to infer past changes in oxygenation, with squares corresponding to laminations, circles to benthic foraminifera species assemblages, and diamonds to redox-sensitive trace metals. Blue shadings indicate a relative decrease in oxygenation and orange shadings a relative increase in oxygenation. The multiproxy data compilation is plotted on top of the expected O_2^{sat} change estimates based on LGM-Holocene changes in sea surface temperature and salinity.

Galbraith, 2013), which ventilate a large portion of the North Pacific thermocline.

Second, it is plausible that the global ocean nutrient inventory decreased across the deglaciation, due to accelerating removal of nitrogen through denitrification (Galbraith et al., 2013), and diminishing input of iron as the atmosphere became less dusty (Winckler et al., 2008). Although it has been argued that a range of negative feedbacks would have prevented very large, durable changes in the nitrogen inventory (Gruber, 2004), it seems likely that nutrient inventories gradually shrank, to some degree, in response to deglacial warming, limiting export production. This suggestion is qualitatively consistent with proxy evidence for particularly high export production during the B/A-ACR in the sub-Arctic North Pacific (Kohfeld and Chase, 2011) and along the western coast of North America (Cartapanis et al., 2012).

Widespread deoxygenation of the upper Indo-Pacific at the onset of the B/A-ACR is expected to have enhanced marine nitrous oxide (N_2O) production drastically (Schilt et al., 2010; Jaccard and Galbraith, 2012; Figure 4). N_2O , a potent greenhouse gas, is produced as an intermediate product in both the oxidation of organic nitrogen (nitrification) under oxic conditions and the reduction of nitrite (denitrification) under suboxic conditions (Freing et al., 2012). The hypoxic and suboxic waters of the northern Indo-Pacific, which may have been almost completely absent during the LGM, are currently responsible for on the order of one-third of the total, natural flux of N_2O to the atmosphere (Hirsch et al., 2006), the rest being contributed by soils in tropical and temperate regions. Simulations with a coupled ocean-biogeochemistry model suggest that atmospheric N_2O concentrations

could have increased by up to 40 ppb when the AMOC strengthened, as it did during the B/A-ACR, due only to changes in marine N_2O emissions (Schmittner and Galbraith, 2008). The fact that proxy indicators show an increase of North Pacific oxygenation following the B/A-ACR, but atmospheric N_2O stayed high, suggests that a small decrease in the oceanic production of N_2O may have been compensated by an increase in the terrestrial source of N_2O .

INSIGHTS ON THE FUTURE FROM THE DEGLACIAL WARMING

The deglacial records clearly show that oceanic oxygen concentrations are sensitive to climate warming. What's more, the changes appear likely to have exceeded the expected decrease of O_2^{sat} in the upper ~ 1 km of the Pacific, while oxygen in the global deep ocean generally increased at the same time. It seems most likely that a decreasing magnitude of O_2^{bio} in the deep ocean drove most of the deep ocean O_2 increase across the deglacial warming, while an intensification of O_2^{bio} in the upper ocean may have exacerbated the decrease of O_2^{sat} . Changes in O_2^{bio} could have been driven by export production, respiration rates, and the ventilation rates of subsurface waters. The sediment records also show that the response to the slow deglacial climate warming was not smooth—the upper Pacific Ocean, in particular, passed through a nadir of low oxygen concentrations during the B-A/ACR, after which the trend actually reversed directions and became better oxygenated.

Most currently used Earth system models tend to show an increase in the volume of hypoxic waters in the upper Pacific over the course of the twenty-first century, as the ocean warms (Cocco

et al., 2012). The deglacial loss of oxygen from the upper Pacific Ocean broadly agrees with this sense of change, despite the deglacial warming having been much slower, and starting from a different initial state. Intriguingly, the upper Indian Ocean gains oxygen in both the model projections (Bopp et al., 2013) and the deglacial reconstruction.

In contrast, the deep ocean oxygenation response to warming in Earth system model projections is opposite that reconstructed for the deglaciation. We suggest three reasons for this apparent discrepancy:


1. This is a consequence of the different rates of warming. The rapidity of anthropogenic warming far exceeds the ability of the deep ocean to take up heat, leading to great strengthening of the thermocline and reduction of vertical exchange. Rapid transient warming may therefore cause deep ocean oxygen to decrease, whereas at steady state, deep ocean ventilation may actually be more vigorous in a warm ocean. In support of this hypothesis, the long simulation of Schmittner et al. (2008) showed a nadir in deep ocean oxygenation about 1,000 years after an increase in CO_2 , after which the deep ocean oxygen concentration started rising.
2. The model ecosystems are missing important temperature-dependent aspects. In particular, the parameterizations of remineralization may be insensitive to temperature and, thereby, miss a decreasing transfer efficiency of organic matter to the deep sea under warming (Matsumoto, 2007).
3. The deep ocean physical circulation changed over the deglacial warming in a way that is not captured by future Earth system model projections. This

could be due to the poor representation and parameterization of Southern Ocean deepwater production and circulation in Earth system models (Russell et al., 2006). Alternatively, deep ocean circulation during the LGM may have differed fundamentally from modern circulation, either due to nonlinearities of ocean circulation at low temperature (Keeling and Visbeck, 2011) or to factors unrelated to temperature, such as changes in tidal mixing.

Finally, we note that reconstructions from the deglaciation may be able to help improve the predictions of future changes in OMZs. Earth system model projections do not agree on the magnitude, or even the sign, of future changes in OMZ volume, most likely due to their inability to simulate the small-scale turbulent features that govern the exchange of shadow zones with neighboring waters (Karstensen et al., 2008; Gnanadesikan et al., 2012). Deglacial records, on the other hand, show strong indications of intensifying denitrification in OMZs (Ganeshram et al., 2000; Galbraith et al., 2013), indicating that warming drove either an increase of remineralization rates within OMZs, a volumetric expansion, or both. Increasing the coverage of records in sediments adjacent to OMZs would help to place firmer constraints on their deglacial intensification, and could help to determine sources of disagreement in future projections.

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